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XXXIII.—*On the Teleostean Affinities of the Genus* Pleuracanthus. By JAMES W. DAVIS, F.G.S. &c.

I PURPOSE in the following remarks to consider certain characteristics in a group of fishes now extinct, but whose fossil remains are found imbedded in the shales and coals of the Carboniferous series of rocks and in the marl slate of Permian age occurring in some parts of Germany. In the latter the fishes are found well preserved and more or less perfect. The anatomy of the fish and the relations of its various parts to each other are clearly defined. In the English Coal-measures, however, the fish has not been preserved so perfectly, and, as a rule, the spines and teeth are found generally distributed where fish-remains have been discovered to exist, but the remaining parts of the skeleton are wanting. The cannel coal between Bradford and Wakefield has yielded some specimens of the bones of the fish, in addition to a large and varied collection of spines and teeth. Prof. Agassiz described the spines of these fishes, and named them *Pleuracanthus* and *Orthacanthus*; and the teeth he also described, and designated *Diplodus*. The continental specimens were first described in 1847 by Dr. Goldfuss of Bonn, as *Orthacanthus Dechenii*. A year later Prof. Beyrich wrote a treatise on the same fish, naming it, however, *Xenacanthus Dechenii*. In 1855 Sir Philip Egerton pointed out that the spine *Pleuracanthus* and the *Diplodus*-teeth belonged to the same genus of fish, and that the *Xenacanthus* of Beyrich was evidently the same; and, further, that *Orthacanthus*, from the great difference in the position of the denticles which extend along its dorsal margin, might constitute the only additional genus to *Pleuracanthus*. Since then a number of intermediate species have been discovered, which conduce towards proving that there can be no real division between *Pleuracanthus* and *Orthacanthus*, and that, consequently, the latter must be absorbed in the former.

The Bohemian specimens of *Pleuracanthus* appear to have been about 18 inches in length. They had a broad flat head, which contracted somewhat towards the body, the latter being narrower laterally, but of greater thickness from the dorsal to the ventral surfaces, and gradually tapering towards the tail. There were two pectoral and two ventral fins; and a dorsal fin extended along the back; beginning immediately behind the head, it encircled the tail and extended along the ventral aspect, nearly or quite to the position of the ventral fins. In front of the dorsal fin there was a straight fin-ray or spine about 5 or 6 inches long in a fish of the size mentioned; it was inserted in the neck, and appears to have been supported by muscles or cartilage, there being no process for articulation to a bony support. The spine in some instances possesses a row of denticles along each lateral surface; and in others the two rows of denticles are placed on the back of the spine and approximate closely to each other. It is composed of very close-grained, dense, bony substance, and, to all appearances, was not immediately connected with the dorsal fin. Besides these two varieties of the spines, which are found attached to the fossil fishes of the Continent, and which were originally described by Agassiz, in the 'Poissons Fossiles,' from detached spines found in the Coal-measures of Britain, others have been discovered in America, and described by Dr. Newberry in the Geological Survey of Ohio, also from the Coal-measures; and during the last year or two I have been fortunate in finding, in the cannel coal of West Yorkshire, other specimens with the denticles in various intermediate positions between the lateral (or *Pleuracanthus* type) and the dorsal (or *Orthacanthus* type), which go far to prove that this difference in the position of the rows of denticles is not of generic importance, and that the two must be united in the genus *Pleuracanthus*. I have expressed these views more fully in a paper recently read before the Geological Society of London.

The body of the fishes in some of the specimens was covered by minute rhomboidal plates of enamel; in the majority, however, this is not preserved and does not appear to have been present, the skin being naked. The head, much depressed, was very broad, and terminated in a rounded snout. The position of the eyes is not indicated in any of the fossils. A pair of orifices, placed a little distance behind the snout, appear to indicate, in the opinion of Dr. Goldfuss, that they may have been connected with the nostrils. The mouth extended in a semicircular form round the anterior portion of the head, the lower jaw projecting somewhat beyond the upper and being of very massive construction. The mouth was armed with several rows of closely-set, three-pronged, sharp teeth, extending one behind the other along each jaw, in a similar manner to those of the Sharks and Rays of existing species. These, found separately in England, were described by Prof. Agassiz, under the generic name of *Diplodus*.

The skeleton of the fish was, for the most part, cartilaginous. The vertebræ were wholly so; but attached to them were bony ribs, short and slender. Connecting the spinal column and the dorsal fin were hollow (?) spinous and interspinous bones, which are preserved and were similar in character to the other hard parts of the skeleton, being composed of cartilage with innumerable osseous centres, the chondroid bone of Prof. Williamson.

Dr. Kner says it is certain that four or five gill-arches, set with a few long rake-like teeth, were present, the larger ends of which were surrounded by many slender gill-rays; they were attached to the horny substance of the bones supporting the tongue. The connexion of the gill-supports with the shoulder-girdle resembled that of the Squalidæ. The shoulder-girdle does not join immediately up to the bones of the head, and is not united with the vertebral column, but, as in the cartilaginous fishes, it is situated so far back that several of the vertebræ are in front of it. Kner discovered three separate bones composing the shoulder-girdle, viz. the clavicle, scapula, and suprascapula; whilst attached to these is a large, broad, bony plate composed of a single piece, which, in the hinder third part, is bent on its outer edge at right angles in the form of a knee; from this springs an articulated straight ray, which extends the whole length of the pectoral fin. From the outer side of the articulated ray spring many fin-rays; and on the inner side there are also a number of weaker rays. Altogether they form a very large and expanded pair of pectoral fins. In an example of the pectoral fin from the shale above the West-Riding cannel coal the fin-rays are very strong, and placed near together. They present the characteristic chondroid structure; and each ray is composed of a number of separate segments, which do not appear to have been joined together except by the investing cartilage of the fin; the ends of the segments present no articulating surface. The structure of the pectoral fins of *Pleuracanthus* may be advantageously compared with the fin of the mud-fish (*Lepidosiren*).

The posterior or ventral fins are built up from the pelvic girdle in a manner similar to the pectoral. There is a pair of peculiar ventral shields, studded over with hook-like appendages, whose use has not been clearly defined. In some of the examples the ventral fins are much nearer together than in others; and where this is the case the bony appendages are absent. It was suggested by Prof. Geinitz, in his great work 'Der Dyas,' that the ventral shield might have been a sucker; and he believed the genus to have been allied to *Cyclopterus*. Dr. Kner, after examining all the specimens then accessible, came to the decision that the ventral appendages were hooking-organs, similar to the claspers found in sharks and in the sheat-fishes or Siluroids of the present day—this explanation being rendered probable from the fact that some of the fossil fishes are provided with appendages, whilst others are devoid of them, leading to the supposition that where the appendages were present the fishes were males, whilst the females would be the fishes without them.

The vertebral column was continued from the pelvis to the extremity of the caudal fin in a straight line. The vertebræ were cartilaginous and are not preserved. The rays supporting the fin were to some extent osseous, and are distinctly shown in some of the specimens.

The systematic position of *Pleuracanthus* is one very difficult to define. The thick cartilaginous ventral appendages incline to a resemblance to the Sharks; but in the structure of the skeleton, and especially in that of the fins, it does not in any way resemble the Sharks. The osseous rays and interrays which support the dorsal fin (the latter also being supported by bony fin-rays), the bony ribs with expanded bases for attachment to the vertebræ, and the possibility, indicated in some specimens, that some of the vertebræ themselves had osseous centres, all remind us of a strong resemblance to the type of bony fishes. The identification of the gill-arches bearing teeth, the projection of the gill-rays, and the presence of teeth attached to the bones of the throat also characterize bony fishes. Against these Teleostean resemblances may be placed others which are again closely related with cartilaginous fishes, for example, the mosaic-like structure of the integument—though some of the Siluroid fishes are possessed of a rough skin almost like the shagreen of the sharks, and one very curious genus (*Sisor*) has the whole length of its back mailed with enamelled scales. The position of the shoulder-girdle, the suspensory jaw, and the attachment of the upper to the under jaw are similar to those of the Plagiostomous fishes. The spine, situated immediately behind the head, solid and circular or flattened in form, without the fin-investing hollow of the commoner *Ctenacanthus* or *Gyracanthus*, does not resemble the fin-spine of any existing shark; but, as was pointed out by Dr. Goldfuss, and afterwards insisted on by Prof. Beyrich, it appears to be closely related to the Rays (*Squatina*) both in form and method of attachment.

Many of the Siluroid fishes have spines very closely approaching those of *Pleuracanthus*; and it may be well to notice one or two examples. *Rita Buchanani*, Cuv. & Val., is about 7·5 inches in length. The head, covered with strong dermal plates, is 1·75 inch across, and very broad and depressed in comparison with its depth. The mouth is at the termination of the snout; it is large and has a wide gape; its jaws are armed with a large number of minute teeth; and others cover the palatal region of the mouth. The eyes are small. From the head the body of the fish tapers rapidly towards the tail. The skin is scaleless. There are two dorsal fins: the anterior one, situated 2·5 inches from the termination of the snout, is armed with a strong articulated spine; the posterior one is an adipose fin without rays. There are two pectoral, a pair of ventral, an anal, and the caudal fins. The pectoral fins are protected by strong bony spines. The features of peculiar interest lie in the spines attached to the anterior dorsal fin and the two pectorals. The latter are 1·6 inch in length and ·2 of an inch broad; they are somewhat flattened, slightly curved, and end in a point. The upper and lower faces are very finely striated; and the two lateral extremities are armed with rows of recurved, long, sharp denticles, extending the whole length of the spine, but becoming smaller near the base. The dorsal spine is 2 inches in length, and of about the same diameter as the pectorals; it is much rounder than the pectorals, and tapers rapidly to a point. It curves slightly backwards, and on its posterior median surface has a single row of denticles extending ·6 of an inch towards the base; the anterior surface is produced so as to form a median keel, which extends all the length of the spine; towards the base this keel is corrugated, forming a line of rough granulations. The sides of the spine are slightly striated. All the spines have an internal pulp-cavity, but show no trace of the posterior hollow seen in the Elasmobranchs.

In numerous species there is a dorsal-fin spine, but no spines to the pectorals.

In a small specimen of *Macrones* from one of the Indian rivers there are two pectoral and one dorsal fins which have spines attached. They present a close resemblance to some of the spines of the fossil *Compsacanthus*. The pectoral fins are armed with a strong spine ·5 inch in length. The spine tapers to a point. Its posterior face is straight, the anterior very slightly curved. It is somewhat flattened laterally, and ornamented with longitudinal striæ. On the median posterior surface is a row of denticles, which extend along the whole length of the spine exposed; the denticles are equal in length to the breadth of the spine, sharply pointed and slightly recurved towards the base. Attached to the spine is the pectoral fin, composed of seven or eight bifurcating fin-rays. The *dorsal* spine is about two thirds the size of the pectoral; it is straight, pointed, striated longitudinally, and has on its posterior surface a single row of short straight denticles, which point towards the base of the spine at an angle of 45°. It is not connected with the dorsal fin, but stands detached. It is implanted in a triangular bone formed by a prolongation of the bones composing the occipital region of the head.

As already explained, the spines of the Siluroids are attached by an articulation of greater or less complexity; but I must confess there does not appear to be any thing extraordinary in this difference. In *Pleuracanthus* the spine is adapted in the best way to the cartilaginous skeleton of the fish, whilst in the Siluroids, having a bony and firm base, nothing appears more reasonable than that, during the period of this development or change in the character of the skeleton of the fish, the spine should have been adapted to its support, and have acquired its present method of attachment. There is also the important consideration that the spines of the rays are all similar in character, with two rows of denticles situated on the lateral surfaces of the spine as widely separated as is possible; whilst those of the Siluroids exhibit every gradation from spines with the two rows of denticles placed laterally, as in the Rays, through many intermediate stages, to those having two rows placed very near together along the posterior surface; in others there is only a single row of denticles along the posterior surface; and, again, there are many examples without any denticles. These variations offer a curious parallelism to the fossil examples; and if, as I have elsewhere hinted, the genus *Compsacanthus* of Newberry, with only one row of denticles, should turn out to be a closely related genus to *Pleuracanthus*, it will be still more so. I have also recently acquired some spines with the same dense structure as the *Pleuracanthus*, and similar in form, but devoid of any denticles so far as I have ascertained, though I have not been able to get one quite clear of the matrix.

In the peculiar group of fishes *Ischyodus* the spine in some respects very much resembles the Pleuracanths; it is situated immediately behind the head, is nearly straight, and has two rows of denticles situated laterally on its upper part. A large proportion of its length is without a fin-groove. Nearer its base, however, there is a cavity for the fin which extended behind the spine. Its base is expanded into a rounded articulating surface, and fits into a socket composed of a strong cartilage springing from the vertebræ—an arrangement which allows of very considerable motion, and enables the fish to elevate and depress its spine at will. The joint is similar in the main to that of the Siluroids, but is less complex and devoid of the interlocking apparatus characteristic of that group. The *Ischyodus* occurs in the Lias and Chalk formations; and though the Chimeroids offer few resemblances to either the Pleuracanths or Siluroids, its spine appears to occupy, in some respects, an intermediate place between the two.

As already observed, the position of the eyes in *Pleuracanthus* has not been identified. This may be due in great measure to the parts surrounding the orbit being of a soft cartilaginous nature, and filling up the orifice previous to its fossilization; but it may also be well to remember that the eye in the Siluroid fish is very small compared with that of the Sharks or Rays, and for this reason it would be more likely to become obliterated.

There are, then, the following conspicuous points of relationship with the Siluroids:—the long tapering figure of the fish; its broad depressed head with rounded snout and terminally situated wide mouth; the naked skin, or more rarely covered with minute enamelled, rhomboidal, detached plates; the absence of scales; the peculiarities of the spine; the long unpaired fin extending along the back, encircling the straight slender tail, and extending along the ventral surface of the body; the spinous and interspinous bones of the body, and the osseous rays of the fin; the presence of a clavicle in the shoulder-girdle; and the fact of there being branchiostegal rays with teeth attached supporting the gills. In the specimen described by Dr. Goldfuss the two anteriorly-pointing conical cavities are considered, apparently with much reason, to be the nasal cavities; and if this be so, they are of decidedly teleostean character, the nasal orifices of the Plagiostomous fishes being in all cases situated beneath the snout and in the Chimera and Rays close to the angles of the mouth, the mouth and nasal orifice in some instances being connected by a groove.

From a consideration of the peculiarities existing in the fishes composing the genus *Pleuracanthus* we are led to the conclusion that it claims a nearer relationship with the bony fishes than with the Elasmobranchs, though there is equal reason to believe that it possesses many characters in common with the Sharks and Rays. We are therefore further led to place the genus in an intermediate position between the two. The distinguishing characters used in modern classification to distinguish the Sharks and Ganoids, viz. the many-valved muscularly-contracting bulbus arteriosus, the spiral valve of the intestine, and the chiasma of the optic nerves, are of such a perishable nature that they are not likely to be found in fossil fishes. In the absence of these we are driven to select such characters for classification as may be preserved, and to collate them as best we may with those of existing forms. Prof. Huxley, in the tenth decade of the Geological Survey, has pointed out the seeming relationship between some of the Ganoid fishes (so called) of the Old Red Sandstone and the modern Siluroids. In the structure of the head of *Coccosteus* the general arrangement of the bony exoskeleton much resembles that of the tropical fish *Clarias*; whilst the peculiar form of the mandibles, and the expansion of the bony elements usually considered to be homologous with the coracoid and radius of other fishes so as to form a large ventral shield, offer many points of resemblance to the Siluroid *Loricaria*. The Devonian *Pterichthys* is also in several ways closely related to the modern Siluroids; its osseous envelope can only be compared to the box-like cincture of the modern *Ostracion*; and the fossil fish *Cephalaspis* has also certain resemblances to *Callichthys* and *Loricaria*. Prof. Huxley remarks, "At any rate, I think the *primâ facie* case in favour of the Teleostean nature of *Coccosteus* is so strong that it can no longer be justifiable to rank it among the Ganoids '*sans phrase*,' but that even those who will not allow it to be a Teleostean must attach to it the warning adjunct of *incertæ sedis*." And further, "Why should not a few Teleosteans have represented their order among the predominant Ganoids of the Devonian epoch, just as a few Ganoids remain among the predominant Teleosteans of the present day? When it is considered that an ichthyologist might be acquainted with every freshwater and marine fish of Europe, Asia, South Africa, South America, the Indian Archipelago, Polynesia, and Australia, and yet know of only one Ganoid, the sturgeon (a fish so unlike the majority of its congeners that a naturalist might be well acquainted with almost all the fossil Ganoids and yet not recognize a sturgeon as a member of the group), it will not seem difficult to admit the existence of a Teleostean among the Devonian Ganoids, even though that Teleostean should in some, even important, points differ from those with which we are familiar."

The relationship of the peculiar fishes of the Old Red Sandstone to the Siluroids of the present time, so clearly enunciated by Prof. Huxley, and, so far as can be defined with our present limited knowledge, with every appearance of probability and truth, carries back the advent of Teleostean fishes to the earliest geological periods during which fishes are known to have existed. Along with the Ganoids they have the greatest claim to antiquity of all the fishes whose remains have been identified. It is possible that the two groups may have had much in common, and that a common ancestry in some intermediate form may be discovered in still older rocks. In the fishes from the Coal-measures, which form the subject of this communication, there seems to be something very like a bridge, a transitional form between the then predominant Elasmobranchs and the Siluroid Teleosteans. Its affinities appear to be decidedly on the side of the Siluroids; and it may best be considered as a forerunner of that great group of fishes. In geological time *Pleuracanthus* is known to extend from the Lower Coal-measures, through the Middle and Upper Coal-measures, of England and America, occurring in the gas-coals of Bohemia (regarded as intermediate or passage-beds between the Carboniferous and Permian rocks), and up into marl slates of the latter group. It remains to be seen what were the successive steps in development which have resulted in the completely ossified and highly organized Siluroids now existing.